

## Phylogenetic analysis of the *Saturnia*-group (Saturniidae) of genera based on scoli structure of mature larvae

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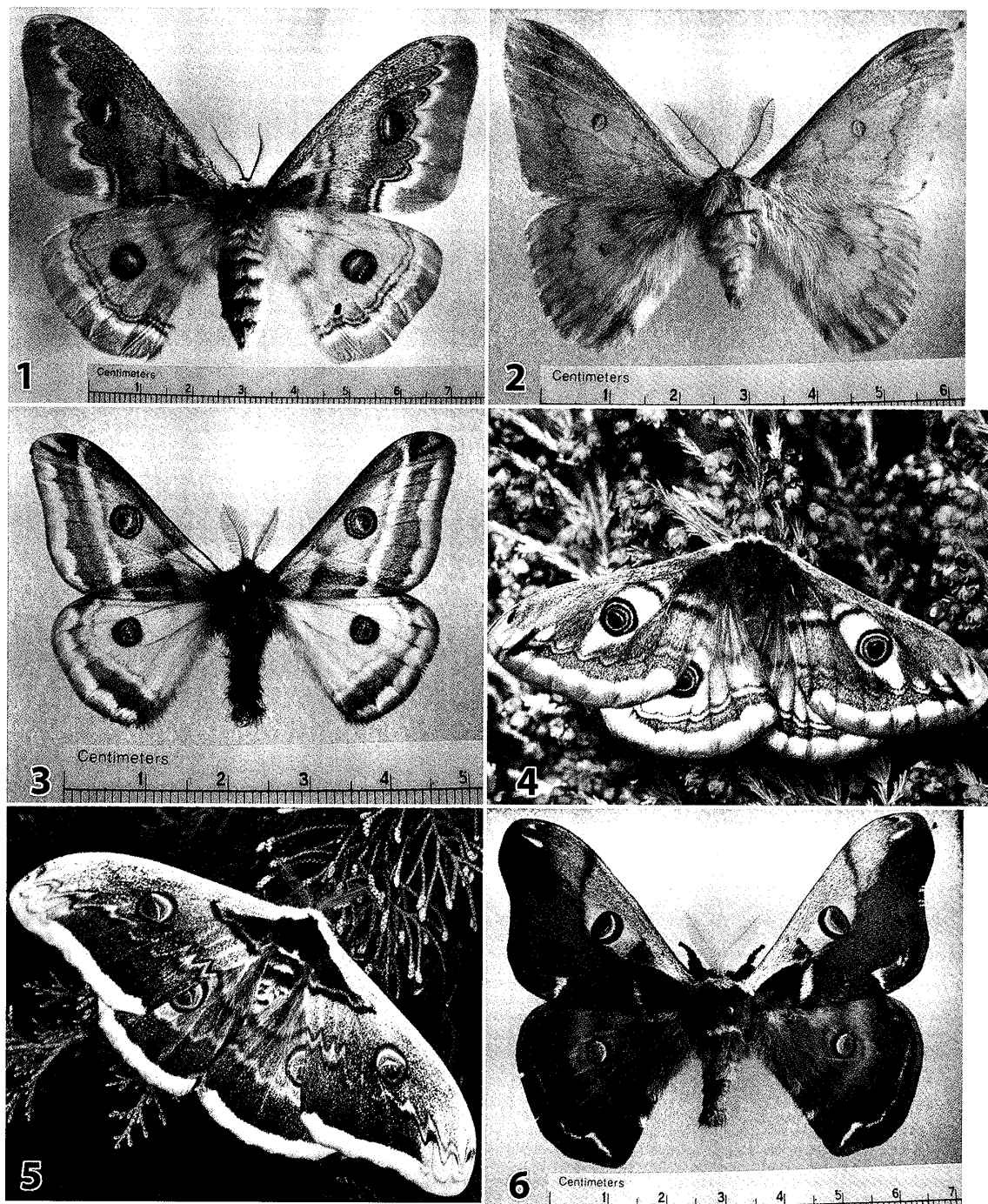
**Abstract** A phylogenetic analysis using final-instar caterpillars of 14 species of Saturniidae was conducted. A total of 22 scoli from 2 thoracic and 4 abdominal segments was categorized according to shape (flat, raised, bulbous) and structure (hairs and spines). Most of the branchings and pairings in the resulting cladogram were supported by previously published classifications. Results support synonymizing *Eriogyna* under *Saturnia* (*sensu stricto*), indicate a close relationship between *Eudia* and *Calosaturnia*, and another clade groups *Perisomena*, *Neoris*, and *Agapema*. The genus *Caligula* as it is currently defined is considered to be polyphyletic.

**Key words** *Agapema*, cladogram, *Caligula*, *Eudia*, *Holocerina*, morphology, *Neoris*, *Perisomena*, *Saturnia*, saturniid, scoli.

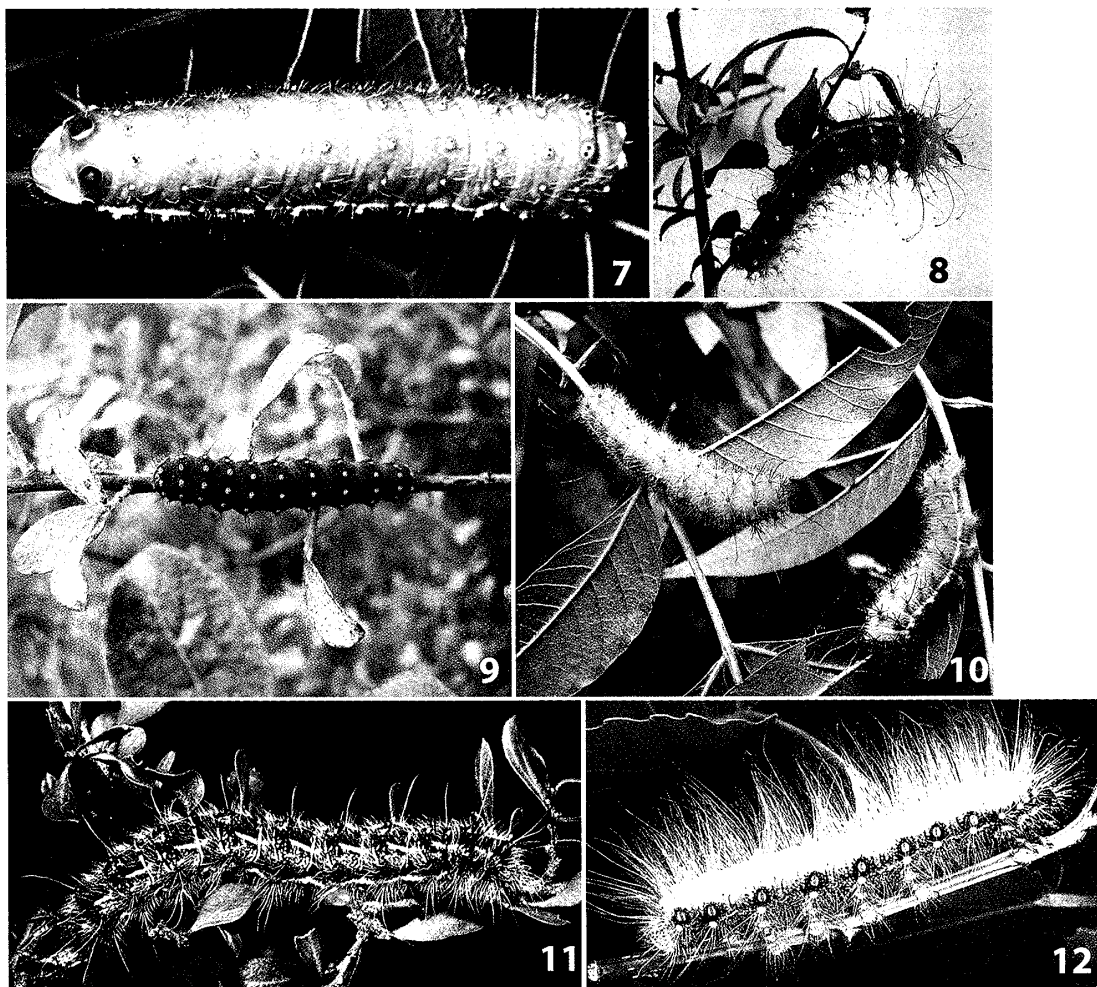
## Introduction

Larval morphology offers a useful tool to those attempting to interpret phylogenetic relationships within various groups of holometabolous insects (Wagner, 2004; Grimaldi & Engel, 2005). Moths of the family Saturniidae, a commonly studied group, are large and attractive (d'Abrera, 1998) and popularly reared. Several species are collected or cultivated for their silk in eastern Asia (Zhu & Wang, 1996). For most species of Saturniidae, the large caterpillars are adorned with conspicuous hairs, spines, and scoli (Deml & Dettner, 2002). These structures are easily studied, and we devised a system to assign character states to them numerically, so that they could be analyzed in a phylogenetic computer program. The resulting cladogram was then compared with other phylogenetic analyses of the same taxa that used molecular or adult morphological data. Therefore, the purpose of this study was to determine the potential value of structure of scoli in mature larvae for reconstructing a hypothetical phylogeny for this set of species.

The *Saturnia*-group of genera is a suite of about 60 known species to which several generic names have been applied, and some of these generic names are still commonly used. Whether one lumps all of these species under *Saturnia* (*sensu lato*), or splits them into several genera or subgenera, several species-groups are recognizable based on geography, larval and adult facies, and cocoon structure. We assume the *Saturnia*-group to be a monophyletic assemblage, although this is not at all certain (Regier *et al.*, 2002). The group is primarily Holarctic in distribution, with a few species ranging down into the Oriental region in the Himalayas. Table 1 lists the species used in this study, and places them in their traditional or restricted generic names, and although we do not accept some of these genus-group names, they are useful in defining *some* of the species-groups that we and all previous workers have accepted as monophyletic. Adults of most of these species were shown in color by Jordan (1911) and d'Abrera (1998), and adults and larvae of four were shown in color by Peigler and Wang (1996). The Japanese species were well-illustrated by Matsumoto (1999). Morphological illustrations (pupae, genitalia) and detailed treatments for the type-species of *Saturnia* and *Eudia* can be found in Jost *et al.* (2005), but the best



Figs 1-6. Examples of adults in the *Saturnia*-group. 1. *Neoris naessigi*, female: Turkey, 40 km NE of Elazig, 1,400 m, 17 Sept. 1992, Martin Geck. 2. *Perisomena caecigena*, male: Slovenia, environs of Kranj, reared in 1982 on *Quercus nigra* by R. S. Peigler in South Carolina. 3. *Agapema galbina*, male: Mexico, Tamaulipas, 46 km W of Soto la Marina, 300 m, emerged 16 Aug. 1994 from wild cocoon collected on *Condalia hookeri* by D. Purdum & K. L. Wolfe. 4. *Eudia pavonia*, female: Spain, Barcelona, Osona, Gurb, reared on *Prunus virginiana* in 1994 by R. S. Peigler in Colorado. 5. *Saturnia pyri*, female: France, Dept. Vaucluse, Gordes, photographed by C. Lemaire. 6. *Caligula jonasi*, male: Japan, Kyushu Island, Fukuoka, emerged 1 Nov. 1982, reared on *Malus* and *Acer saccharinum* by R. S. Peigler in South Carolina. (Specimens shown in figs. 1, 2, 3, & 6 were deposited in Department of Entomology, Texas A&M University.)



Figs 7–12. Examples of mature larvae in the *Saturnia*-group. 7. *Caligula lindia*: India, Jammu & Kashmir, road between Baltal and Sonamarg, reared in 1981 on *Populus deltoides* by R. S. Peigler in Texas. (Note that the pair of scoli on the posterior end plus orange anal plate give the illusion of a small reptile or amphibian, probably to deceive insectivorous birds.). 8. *Saturnia pyri*: France, Dept. Vaucluse, Gordes, reared on *Prunus spinosa* by R. S. Peigler in Texas. 9. *Eudia pavonia*: UK, Scotland, Midlothian Shire, Bevelaw Moss, near Edinburgh, photographed in the field on 14 July 2005 on *Salix aurita* by R. S. Peigler. 10. *Calosaturnia walterorum*: USA, California, San Diego Co., Escondido, reared in 2005 on *Pistacia chinensis* by R. S. Peigler in Texas. 11. *Agapema platensis*: USA, Texas, Kinney Co., Kickapoo Cavern, March 1993, on *Condalia viridis*, photo by Kelly Bryan. 12. *Caligula japonica*: Japan, Honshu Island, Tokyo Pref., Okutama, Mt Tenso, reared in 1981 on *Populus deltoides* by R. S. Peigler in Texas.

available data set for morphology of the Saturniinae is by Rougerie (2005). A selection of mature larvae and adult moths is shown in Figures 1–12, to provide some perspective of the diversity yet similarity of this group. The *Saturnia*-group belongs to the tribe Saturniini within the subfamily Saturniinae. Other genera in the Saturniini, but not in the *Saturnia*-group, include *Actias*, *Argema*, *Cricula*, *Loepa*, *Opodiphthera*, *Copaxa*, *Lemaireia*, and *Antheraea*.

### Previously proposed relationships

Recent workers (*i. e.* Nässig, 1994) have used the generic name *Rinaca* for those species that have long been called *Caligula*. We reject this arrangement by provisionally considering *Rinaca* to be monotypic, containing only its type-species *zuleika*. Until more comprehensive hypothetical phylogenies can be supported with additional molecular and morphological data, we do not consider *zuleika* to be congeneric with those species traditionally placed in *Caligula*, the latter group still containing at least four distinct lineages: 1) *simlaljaponica*; 2) *anna/bieti/lindia/grotei*, and possibly *thibeta*; 3) *jonasi/boisduvali*; and 4) *cachara/heinrichi*. Color figures of Taiwanese endemic taxa representing the first three aforementioned lineages (*arisana*, *okurai*, and *fukudai*, respectively) were given by Fu and Tzuoo (2004). We believe that *Caligula* as currently defined here and traditionally by earlier authors is probably polyphyletic, so it currently makes no sense to try to lump this suite of species-groups under *Rinaca*, an action which cannot contribute toward the eventual goal of nomenclatural stability for generic-group names in the *Saturnia*-group. The generic name *Dictyoploca* has been commonly used for *simla* and *japonica*, but *simla* is the type-species of both *Caligula* and *Dictyoploca*, making the latter name an objective synonym of the former, and therefore unavailable. We did not have larvae of *Rinaca zuleika* (Hope) available for this study.

The smallest moths of the group belong to the genera (or subgenera) *Eudia*, *Agapema*, and *Calosaturnia*. *Eudia* is Palearctic, but *Calosaturnia* contains three species from California with a few records for Oregon and northern Baja California, and some workers (*i. e.* Ferguson, 1972; Lemaire, 1978 and references cited therein) took the opportunity to point out the striking similarity between the adults of *C. albofasciata* and *E. pavonia*. This similarity is partially explained by the diurnal males and nocturnal females in both species, whereas in all other species both sexes are diurnal (*mendocino*, *walterorum*) or nocturnal (*spini*, *cephalariae*, and all *Agapema*). However, the larval morphology and cocoon structure of *E. pavonia* and *C. albofasciata* also resemble each other more than those of the other two *Calosaturnia*. The relationship between *Agapema* and other Saturniini was also discussed by Peigler and Kendall (1994).

A close relationship between *Neoris* and *Perisomena* was proposed by Jordan (1911) and accepted by Peigler (1996), but the molecular work by Regier *et al.* (2002) indicated that *Neoris* may be the most distantly related to all others included in the present study. The name *Eriogyna* is used here to apply to a monophyletic set of species from southeastern Asia, but the wing pattern, larval morphology, and cocoon structure all point to a close relationship to the western Palearctic *Saturnia* (*sensu stricto*), and recent authors (Peigler & Wang, 1996; Naumann & Löffler, 2005) considered *Eriogyna* to be a subjective synonym of *Saturnia*. Incidentally, three taxa within *Eriogyna* that were formerly treated as subspecies of *pyretorum* (Jordan, 1911) were recognized as full, distinct species by Naumann and Löffler (2005), and we concur with their assessment.

### Materials and methods

We decided to use scoli because these structures are easily studied on specimens preserved in alcohol, and they vary minimally among individual specimens. This study utilized only 1–3 specimens of mature caterpillars for each taxon. The source localities for most of our specimens are stated in the legends to our color figures; additionally *E. pyretorum* was from Hong Kong, *E. cephalariae* was from eastern Turkey, *A. homogena* was from southern Arizona, *C. albofasciata* was from southern California, and *H. angulata* was from Transvaal.

Table 1. Species included in the present study.

Species	Distribution	Closely allied species
<i>Saturnia (Saturnia) pyri</i> [Schifferrmüller] (Figs. 5, 8)	s.w. Palaearctic	<i>atlantica</i>
<i>Eriogyna pyretorum</i> (Westwood)	S. Korea, e. China	<i>cognata, cameronensis, cidosa, centralis, pinratanai, luctifera</i>
<i>Eudia pavonia</i> (Linnaeus) (Figs. 4, 9)	pan-Palaearctic	<i>spini, cephalariae</i>
<i>Eudia cephalariae</i> (Christoph)	e. Turkey, Transcaucasus	<i>pavonia, spini</i>
<i>Calosaturnia albofasciata</i> Johnson	California	unclear
<i>Calosaturnia walterorum</i> Hogue & Johnson (Fig. 10)	southern California	<i>mendocino</i>
<i>Caligula lindia</i> Moore (Fig. 7)	Pakistan, n.w. India, s. China	<i>anna, bieti, grotei, tsinlingshanis</i>
<i>Caligula jonasi</i> Butler (Fig. 6)	Japan, Taiwan	<i>boisduvali, witti, chinghaina</i>
<i>Caligula japonica</i> Moore (Fig. 12)	Japan, Far East mainland	<i>simla</i>
<i>Neoris naessigi</i> de Freina (Fig. 1)	e. Turkey	<i>huttoni, shadulla, codyi</i>
<i>Perisomena caecigena</i> (Kupido) (Fig. 2)	s.e. Europe to Transcaucasus	unclear
<i>Agapema homogena</i> Dyar	n. Colorado to s. Mexico	unclear
<i>Agapema galbina</i> (Clemens) (Fig. 3)	s. Texas, n.e. Mexico	<i>anona, platensis</i> (Fig. 11), <i>dyari, pelora, dentifasciata</i>
<i>Holocerina smilax</i> (Westwood)	southern Africa	outgroup in the present study

Caterpillars preserved in 70% isopropyl alcohol were examined under a dissecting microscope and characters coded. The 22 characters selected consisted of the following thoracic (T1, T2–T3) and abdominal (A1, A6, A8, A9) scoli: dorsal, subdorsal, lateral, subventral. As is normally the case (Stehr, 1987: 295), scoli of segments T2 and T3 are similar, A1 is similar to A2, and A6 is similar to A3–A5 and A7. Therefore, we did not tabulate characters for abdominal segments A2 through A5 and A7. Characters 1–22 were as follows: 1. T1 dorsal; 2. T1 subdorsal; 3. T1 lateral; 4. T1 subventral; 5. T2–T3 dorsal; 6. T2–T3 subdorsal; 7. T2–T3 lateral; 8. T2–T3 subventral; 9. A1 dorsal; 10. A1 subdorsal; 11. A1 lateral; 12. A1 subventral; 13. A6 dorsal; 14. A6 subdorsal; 15. A6 lateral; 16. A6 subventral; 17. A8 dorsal; 18. A8 subdorsal; 19. A8 lateral; 20. A9 dorsal; 21. A9 subdorsal; 22. A9 lateral. We deleted the subventral scoli of A8 and A9 because the character state was identical (*i. e.* absent) in all 14 species, so those data were not informative and would thus make no difference in the resulting cladogram.

Each character was assigned one of the nine following character states, with no attempt to assign polarity, and our observations are recorded in Table 2. The ones that we call bulbous correspond to those called tubercles by some writers, and Sternwarzen (meaning star warts) by German authors. It was sometimes difficult for us to distinguish between character states 7 and 8, even on larvae that were not very hirsute.

1. bulbous, with long hairs and short spines
2. bulbous, with short spines only
3. raised, with long hairs only
4. raised, with long hairs and short spines
5. raised, with short spines only
6. flattened, with long hairs
7. flattened, with no hairs
8. absent, or not discernible
9. fused, where two scoli appear to be partially or completely united

Earlier attempts by us to assign polarity and to lump the character states into a smaller number resulted in trees that contained various branchings unsupported by any known charac-

Table 2. Character states for scoli observed in mature larvae of all 14 species.

Species	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22
<i>Saturnia pyri</i>	9	9	1	3	1	1	1	1	5	5	1	1	2	4	1	6	1	1	1	1	1	8
<i>Eriogyna pyretorum</i>	6	6	1	4	1	1	1	4	2	2	1	5	2	2	1	6	2	2	1	1	1	7
<i>Caligula lindia</i>	7	6	4	4	2	4	4	6	5	5	4	7	5	5	5	6	5	5	4	2	5	8
<i>Caligula jonasi</i>	6	6	4	4	4	4	4	6	4	7	3	8	4	6	6	8	3	6	6	3	3	8
<i>Caligula japonica</i>	9	9	4	7	1	4	4	7	1	5	5	7	4	5	4	7	4	5	4	4	4	8
<i>Neoris naessigi</i>	6	6	4	5	3	6	6	5	6	6	6	8	6	6	6	8	6	6	6	6	6	8
<i>Perisomena caecigena</i>	6	6	3	3	1	4	3	6	1	4	3	6	4	4	3	6	3	4	6	4	4	8
<i>Eudia pavonia</i>	9	9	1	4	1	1	1	4	2	1	1	6	2	1	1	6	1	1	4	1	1	8
<i>Eudia cephalariae</i>	9	9	1	4	1	1	1	4	2	1	1	6	1	1	1	6	1	1	4	1	1	6
<i>Calosaturnia albofasciata</i>	9	9	1	6	1	1	1	6	1	1	1	8	2	1	4	7	1	1	4	1	1	8
<i>Calosaturnia walterorum</i>	4	5	5	7	2	2	4	6	2	1	5	7	5	1	4	7	2	2	4	2	5	8
<i>Agapema homogena</i>	6	4	3	3	6	7	8	3	7	6	6	7	6	6	6	8	6	6	7	7	7	7
<i>Agapema galbina</i>	6	6	3	3	4	3	6	6	4	4	7	7	7	7	7	7	4	7	7	4	7	8
<i>Holocerina smilax</i>	3	1	4	7	3	1	1	6	4	4	4	7	4	4	4	7	4	4	4	4	4	7

ters. The data set used for phylogenetic analysis consisted of scoli characters conceptually translated by MacClade 4, version 4.06 (Maddison & Maddison, 2003). Maximum parsimony analysis of the data set was conducted using *PAUP\** 4.0b10 (Swofford, 2002) using unordered, equally-weighted character transformations. An heuristic tree search with an initial max tree setting of 10,000 using tree-bisection-reconnection branch swapping with 100 replicates of random taxon-addition sequences was performed, and only the best trees were kept. When rooting the unrooted tree, we made the ingroup monophyletic and the outgroup paraphyletic with respect to the ingroup (Hall, 2004). *Holocerina smilax* was defined as the outgroup, because it is believed to be a more basal representative of the subfamily Saturniinae (Regier *et al.*, 2002).

## Results and discussion

Of the 162,666 rearrangements found in the heuristic search, the two most parsimonious trees were retained. The strict consensus of the two most parsimonious (MP) trees was found in the heuristic search. One of the trees showed the same topology as one of the MP trees, but differs from the other MP tree by having a polytomy. The tree that was better resolved at the clade (*pyri*+*pyretorum*)+ (*pavonia*+*cephalariae*) was therefore selected to show in Figure 13.

The close relationship between the western Palearctic *Saturnia* (*sensu stricto*) and the eastern Asian *Eriogyna* is supported by our results, and we consider that the latter name should be treated as a synonym of the former. Regarding the relationships between *Agapema*, *Neoris*, and *Perisomena*, our results place those three close, supporting earlier hypotheses (see above) and arguing for further study on these groups. The position on our tree (Fig. 13) of *Calosaturnia walterorum* is unexpected and inconclusive, and is likely erroneous (see below). For the species currently classified under *Caligula*, our results suggest this genus to be polyphyletic. Aside from our data set, the cocoons, general appearance of larvae, and adult wing patterns also all agree with our results that *Caligula jonasi* (and its allies *boisduvali*, etc.) may indeed be phylogenetically closer to *Neoris* than to *Caligula japonica* (and *simla*) or *Caligula lindia* (plus *lindia*, *bieti*, *grotei*, *anna*, etc.). The close relationship between *Saturnia* (*sensu stricto*) and *Eudia* has long been demonstrated by many successful hybrid crosses in captivity (Jordan, 1911: 223), but this could simply be an artifact of greater availability of livestock of those European (*pavonia*, *pyri*, *spini*) and north-west African species (*atlantica*) to the workers who made the crosses. It is likely that many

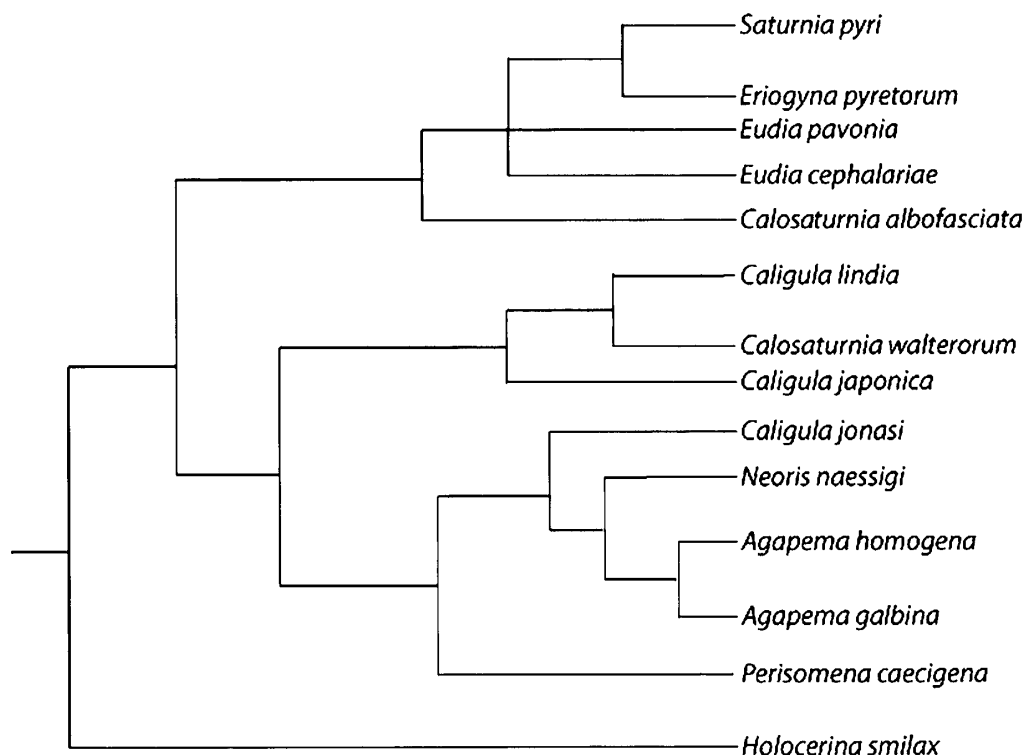


Fig. 13. Cladogram showing hypothetical phylogeny based on scoli of mature larvae. Tree length 122, consistency index 0.77, retention index 0.70.

successful crosses between the European species and those from central and eastern Asia could also be reared.

The primary question for the Nearctic taxa is whether *Agapema* is monophyletic with (*i. e.* the sister-group to) *Calosaturnia*, or if these groups represent two separate dispersal events from eastern Asia via Beringia. We believe that all three *Calosaturnia* probably form a monophyletic lineage, a plan supported by morphology (Lemaire, 1978) and molecular data (Regier *et al.*, 2002). However, our results open the question of whether *C. albofasciata* may be more closely related to *Eudia*, indicating an even more recent (*i. e.* a third) dispersal from Asia, but it must be remembered that some similarities observed between *E. pavonia* and *C. albofasciata* may be plesiomorphic or convergent, underscoring the importance of defining polarity in characters. One previously unreported parallel between these groups is that cocoons are sometimes spun in terminal branches or inflorescences of the host plants: this has been observed in *Eudia pavonia* in Germany (Schmitt, 2000), *Calosaturnia walterorum* in California, and by us in *Agapema dyari* in western Texas. Unfortunately, *Eudia* was not included in the molecular study by Regier *et al.* (2002).

We note that the two main clades in our results (Fig. 13) correspond to two categories of a cocoon character that would appear to be insignificant and probably highly plastic and therefore easily reversed. Cocoons of those in Clade 1 (*pyri*–*albofasciata*) have solid walls, whilst those in Clade 2 (*lindia*–*caecigena*) construct reticulate cocoons, with tiny net-like openings. Moreover, larvae in Clade 2 are also generally much more hirsute than those in Clade 1, but *C. lindia* and *C. walterorum* are exceptions.

In conclusion, we do not believe that our results shown in Fig. 13 represent the exact phylogenetic relationships of the taxa included in our study. However, some groupings are appar-

ently correct, which is instructive in showing the value of gross anatomy of caterpillars alone in such studies, and this was the primary purpose of this project. Our results are likewise useful to demonstrate the importance of using as many characters as possible from as diverse a data set as available when conducting phylogenetic work. Although combining molecular, morphological, and behavioral data is the most desirable approach, even diverse and larger data sets do not always yield definitive results, as shown by Ylla *et al.* (2005) in a study of moths in the same tribe as the *Saturnia*-group.

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## 摘 要

終齢幼虫の肉瘤に基づく *Saturnia* グループの属の系統解析 (Robert A. MIRANDA and Richard S. PEIGLER)

ヤマユガ科の14種の終齢幼虫について、胸部2環節、腹部4環節の計22の肉瘤を類型分けし、*Saturnia*, *Eudia*, *Eriogyna*, *Calosaturnia*, *Perisomena*, *Neoris*, *Agapema*, *Caligula* の系統解析を試みた。使用した肉瘤は、前胸と中胸(中胸と後胸はほとんど同じ)、第1腹節(第2腹節もほぼ同様)、第6腹節(第3–5腹節もほぼ同様)、第8腹節、第9腹節で、これらを形状および構造に従って区分けした。系統解析の結果は図示した通りとなったが、現在の属 *Caligula* は多系統と考えられた。

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